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Habitat dimensions of Diplopoda in a temperate forest on acid soil

BY

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Synopsis: The relationships between the descriptors of twelve forest sites and the composition of the Diplopod communities are studied, in particular by correspondence analysis. Soil texture, soil acidity and waterlogging are important habitat dimensions for most of the Diplopod species.

Keywords: Diplopoda – Habitat – Temperate forest – Correspondence analysis.

INTRODUCTION

Twelve Diplopod communities in the forest of Orleans (France), including fourteen species, were sampled in autumn and spring from October 1985 to May 1987 (DAVID, 1989). Their composition is recalled in Table I, together with the composition of four communities previously sampled in the same sites (Nos. 2 *a*, 6 *a* and 10 *a* in the autumn of 1981 and spring of 1982; No. 1 *a* in the autumn of 1984 and spring of 1985). In this paper, the twelve corresponding sites are described and the relationships between the site descriptors and the composition of the Diplopod communities are studied, with the purpose of defining the main habitat dimensions of species.

The habitat of an organism is the place where it lives, "its address" (ODUM, 1971), and this term, when applied to a species, means the range of environments in which it lives. To define the habitat dimensions of a given species consists in finding, among all the environment descriptors, those which are critical for it, and in measuring its response (*e.g.* its abundance) with respect to those

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particular descriptors. In other words, the question is what site descriptors are correlated with species' abundances.

This concept of habitat can be used on different scales (macrohabitat or microhabitat – *op. cit.*) but, in accordance with WHITTAKER *et al.* (1973), it will only concern inter-community (inter-site) variables in the present paper. Intra-community (intra-site) variables are regarded as niche variables and will not be dealt with here. For example, if two Diplopod species only live in deciduous forests, the nature of the litter may be critical for them and they have this habitat dimension in common; where they coexist, it is possible that one lives in leaf litter and the other in rotting wood, but it will be considered that they have "the same address" in spite of their intra-community difference.

Former studies of the main habitat dimensions of Diplopoda divide into two types:

– *Experimental approaches* trying to demonstrate the effect of one factor on the natural distribution (BARLOW, 1957; THIELE, 1959; HAACKER, 1968; O'NEILL, 1969; ENGHOFF, 1976; PEDROLI-CHRISTEN, 1977; WEGENSTEINER, 1982; GROMYSZ-KALKOWSKA & TRACZ, 1983; MEYER & EISENBEIS, 1985; VOIGTLÄNDER, 1987; and, indirectly, behavioural or physiological studies by CLOUDSLEY-THOMPSON, 1951; PERTTUNEN, 1953; STEWART & WOODRING, 1973). Most of these authors succeed in interpreting some cases but fail in others (*cf.* BARLOW, 1957; HAACKER, 1968). That can be explained by arbitrary selections of the studied factors. But, even supposing that they are determining for a given species, this approach has the drawback of being extremely analytic, of dealing with one factor out of context; in particular, it seldom makes it possible to foresee animals' responses under conflicting conditions, for the study of combined factors requires an amount of work which has seldom been achieved. On the other hand, laboratory experiments are likely to provide objective data which have to be taken into account in any interpretation.

– *Descriptive approaches* try to precise species' distributions in an area and to find relationships with the environment descriptors, so as to speculate about those that might be actual factors of distribution (BLOWER, 1956; BRENY & BIERNAUX, 1966; BIERNAUX, 1972; ENGHOFF, 1974; DUNGER & STEINMETZGER, 1981; PEDROLI-CHRISTEN, 1981; STEINMETZGER, 1982; SIMONSEN, 1984; KIME & WAUTHY, 1984). But, to be safe from criticism, this type of study should fulfil three conditions. 1) Sampling must provide reliable data about the presence or abundance of species. 2) The description of sites must be as systematic and complete as possible; one cannot be satisfied with a few descriptors (*e.g.* temperature and humidity), and the inter-site differences must be measured rather than inferred from "biological indicators" like the nature of the vegetation. 3) The relationships between descriptors and species must be checked with the help of a diagram or a statistical test. Conceived as above, a descriptive approach makes possible a valuable statement of species' habitat in the studied area, even if all difficulties are not over. First, because this approach is extremely synthetic, and it would be necessary to know all site descriptors (inclusive of the whole fauna and microflora) in order to conclude. Secondly, because different descriptors are often associated, and it is then difficult to know the one which is actually involved in a correlation. Lastly, because a correlation is never a proof, and every result from a descriptive approach needs an experimental confirmation. Even if a species seems closely linked to some site conditions, one must notably bear in mind that these are not necessarily advantageous *per se;* in these conditions, interactions with other animal species (competition, prey-predator relationship) might simply be more favourable (CLOUDSLEY-THOMPSON, 1962).

In point of fact, field observations and laboratory experiments complement one another, and a two-way investigation is necessary to tackle this kind of problem. From this point of view, the field study carried out in the forest of Orleans can throw light on the matter, but not be deciding.

I. – METHODS

A) Description of the sites

The study concerns the Ingrannes Massif (13,600 ha) in the State forest of Orleans, with acid and generally hydromorphic soils, located on sand and clay of Sologne. The twelve sites, 400 m^2 each, are within a radius of 5 km, on the parcels Nos. 921 (1), 697 (2), 808 (3), 875 (4), 660 (5), 740 (6 and 10), 848 (7), 775 (8), 781 (9), 842 (11) and 805 (12). The descriptors that might be related to Diplopod distribution, according to literature, were all measured during the sampling period of 1985-1987.

1) *Nature of the leaf litter*

Five units of dead leaves from the AoL layer, 1/16 m^2 each, are taken in each site in April, when the leaf fall is finished for deciduous trees, sessile Oak included, and when most of the soil animal populations begin a new cycle of activity. Leaves are washed in tap-water, sorted according to tree species, and dried at 105°C for 48 hours. The amount of each tree species is expressed in percentage of the total dry mass (herbs and mosses excepted).

2) *Nature of the herb and moss layers*

The area covered by each herb or moss species is estimated in each site during summer, then expressed in percentage of the total area.

3) *Texture of the upper soil layer*

Five units are taken in the upper soil layer of each site (0 to −5 cm), then mixed to constitute a mean site sample. Analyses for sand, silt and clay percentages are made by densimetry in a specialized Laboratory.

4) *Climatic descriptors*

Independently of the mean climatic conditions in the forest of Orleans, inter-site differences are searched for, mainly at times of the year when some factors can be limiting for soil fauna:

– *Depth of the water table* is measured during the cold season, from December to April, when it can prevent animals from burrowing. Measures are made with three 1 m deep piezometers per site, on the same days in all the sites.

– *Soil dryness* is measured in summer, when water tables disappear and there is a tendency for soil to become drier and drier in spite of precipitations. Soil moisture is first measured each month, from July to September, on the same days in all the sites, by weighing soil units (0 to −5 cm) before and after drying at 105°C. Then, the mean soil moisture in summer (SM) is compared to field capacity (FC) at pF=2.5 and wilting point (WP) at pF=4.2, to take into account the soil texture of each site

(VANNIER, 1971). *Relative moisture deficit* is calculated as:

$$\frac{\mathrm{FC}-\mathrm{SM}}{\mathrm{FC}-\mathrm{WP}} \times 100.$$

– *Mean temperature* $[(T_{max} - T_{min})/2]$ is compared in the different sites on four occasions in summer and four in winter. Measurements are made in all the sites simultaneously, with twelve maximum and minimum thermometers set in the shade at ground level.

– *Openness of the forest stand*, which has an influence on temperature and the amount of light reaching the ground, is estimated in summer with the following scores:

1: Closed (covering above 90%);
2: Not very open (covering between 75 and 90%);
3: Semi-open (covering between 50 and 75%);
4: Open (covering between 25 and 50%);
5: Very open (covering between 10 and 25%)

5) *Features of the humus*

The types of humus are compared in the different sites by measuring the mean thickness of the AoL (complete leaves), AoF (underlying pieces of leaves) and AoH (fine organic matter not mixed with minerals) layers. Moreover, five soil units per site (0 to -5 cm), mixed to constitute a mean site sample, are analysed in a specialized Laboratory for several parameters of the A_1 layer: *pH in water; percentage of organic matter;* carbon (C) and nitrogen (N) percentages of this last, in order to calculate its *C/N ratio*.

B) Data analysis

1) *Community analysis*

Table I is processed by correspondence analysis (CA) (BENZECRI, 1973; GREENACRE, 1984). This method of multidimensional ordination can process arrays of non-normal data, even if they contain a number of zero counts (LEGENDRE & LEGENDRE, 1984). However, it is better that the masses of rows and columns shoud not be too different from each other, and, for this purpose, the densities (d) of the Diplopod populations are transformed into log $(d+1)$. Previously, the species merely present in each site (listed + in Table I) are arbitrarily allocated a density of 0.1 Ind./m^2.

The computer programme gives, in addition to the co-ordinates of communities and species on each principal axis, their absolute and relative contributions.

The communities sampled in previous years (Nos 1 *a*, 2 *a*, 6 *a* and 10 *a*) are projected as supplementary columns (which do not play any part in determining the principal axes).

Axis interpretation is carried out in two ways:

– First, by projecting the site descriptors as supplementary rows. Previously, each descriptor is divided into two supplementary rows (*e.g.* pH+ and pH–), and its values (y) are standardized on a scale from 0 to 1 as follows:

$$\frac{y-y_{\min}}{y_{\max}-y_{\min}}\ (\text{for}+)\ \text{and}\ \frac{y_{\max}-y}{y_{\max}-y_{\min}}\ (\text{for}-)$$

After projection, one searches graphically for +/– oppositions in line with the principal axes: they are the best for an interpretation. This searching is made easier by an examination of the relative contributions, because the closer onto an axis a descriptor is projected, the higher is the relative contribution of this axis to it.

TAB. I. — **Composition (Ind./m²) of the Diplopod communities in twelve sites of the forest of Orleans, in 1985-87. Nos. 1 a, 2 a, 6 a and 10 a are homologous of Nos. 1, 2, 6 and 10 in previous years** (see text). + indicates the presence of species of very low density, only underscored by trapping (from DAVID 1989).

	Site No.															
	1	2	3	4	5	6	7	8	9	10	11	12	1 *a*	2 *a*	6 *a*	10 *a*
Polyxenus lagurus. .	.	0.1	0.9	.	1.1	8.9	2.7	8.5	6.2	2.7	0.1	.	.	.	1.1	14.7
Polyzonium germanicum.	0.9	16.9	20.4	.	137.9	22.2	15.1	2.7	334.2	166.4	60.4	.	+	60.7	122.2	779.6
Chamaesoma brolemanni.	0.9	.	.	12.4	.	.	.	.	.	.	.	1.8	9.6	.	.	.
Chordeuma silvestre.	.	.	.	2.7	.	.	.	.	1.8	.	.	0.9	.	.	.	.
Microchordeuma gallicum.	.	9.8	0.9	.	6.2	1.8	.	.	2.7	8	.	.	.	25.9	24.9	35.4
Polydesmus angustus.	19.3	6.4	2.7	1	5.5	2.7	0.9	2.7	14.3	1.9	+	0.9	43.1	8.2	36.5	16.1
Tachypodoiulus albipes.	+	4.4	+	+	0.9	+	1.8	0.1	.	+	.	1.8	+	3.7	3.4	.
Ommatoiulus sabulosus.	.	.	.	.	.	.	.	.	0.9	.	.	.	.	0.2	0.2	0.8
Cylindroiulus nitidus.	4.6	47.2	.	.	.	.	.	.	.	.	.	.	19.1	55.8	.	.
Cylindroiulus londinensis.	5.4	1.8	5.3	.	3.6	0.9	0.9	0.9	.	0.9	4.4	1.8	6.8	4.6	+	.
Cylindroiulus punctatus.	1.2	1.2	.	3.1	2.1	.	.	.	.	.	.	.	0.3	0.6	.	.
Leptoiulus bruyanti.	.	.	20.4	.	.	.	18.7	3.6	.	.	.	.	.	.	.	.
Glomeris marginata.	52.2	3.6	+	2.7	10.7	1.8	.	1.8	1.8	3.6	0.9	4.4	14.1	1	1.6	0.4
Glomeris intermedia.	11.6	1.8	1.8	.	5.3	+	.	1.8	.	5.3	.	0.9	5.7	1	6.8	0.6

– Secondly, the interpretation of the axes is checked by calculating coefficients of linear correlation, between the ordinations of communities on each axis and the site descriptors.

2) *Single species analysis*

For the least characteristic Diplopod species, the analysis of data is pursued further by calculating coefficients of linear correlation, between the absolute density of the Diplopod populations (transformed into logarithms) and the site descriptors. When a correlation with one descriptor is significant, coefficients of partial correlation excluding the influence of the former are calculated, in order to find a possible correlation with a second descriptor.

The coefficient of determination is also calculated to measure, among the variation in a given species' abundance, the proportion which can be explained by one descriptor (simple R^2) or a linear combination of two descriptors (multiple R^2) (LEGENDRE & LEGENDRE, 1984).

II. – RESULTS

A) Description of the sites

The values of the twenty-four main descriptors of the twelve sites are given in Table II: nature of the leaf litter, covering by the most abundant herb and moss species, texture of the upper soil layer, climatic descriptors and features of the humus. With regard to temperatures, only those of summer are given, when a slight but significant gradient of 2.35°C exists between sites Nos. 4 and 10; in winter, no significant difference in temperature has been found.

Some of these descriptors are different aspects of one and the same phenomenon. That may be the case whenever they are associated by an obvious linear relation (positive or negative), which can be shown by examining the scatter diagram for every pair of descriptors, then calculating their coefficient of correlation. The most strongly associated descriptors (with highly significant r; $P<0.01$) are given in Figure 1. In such cases, if the abundance of a Diplopod species is correlated with one of these descriptors, it is thereby correlated with the others, without an exact knowledge of the one which is an actual factor acting on the species – assuming that this factor exists. For example: the most open sites have also Scotch Pine (*P. sylvestris*) and Bracken (*P. aquilinum*) in abundance, and are warm during summer; the sites with a high pH value have also a not very thick Ao or AoH layer, and Bramble (*R. fruticosus*) in abundance, etc.

B) Community analysis by C.A.

1) *Interpretable axes*

Nearly three quarters of the variation in Diplopoda's abundances in Table I can be summarized with three principal axes. The percentages of inertia along these axes are 35.8, 21.6 and 16% respectively, adding up to 73.4%. The percentage of inertia along the fourth axis is much lower (8.4%). As a result, the ordinations in reduced spaces will be studied in planes defined by the three first principal axes.

TAB. II. – **Description of the twelve sites.**

	Site No.											
	1	2	3	4	5	6	7	8	9	10	11	12
Leaf litter (%)												
Quercus petraea (+ *robur*)	79	96	88	89	72	44	4	32	1	1	7	1
Fagus sylvatica	19	.	.	1	.	.	.	36	1	.	.	.
Carpinus betulus	2	2	12	10	6	8	64	2	.	.	.	.
Betula verrucosa (+ *pubescens*)	.	2	.	.	.	7	.	1	12	1	.	.
Pinus sylvestris	.	.	.	.	20	41	32	30	86	98	93	99
Herbs and mosses (%)												
Hedera helix	2	14	12	1	5	7	2	1	.	.	.	.
Rubus fruticosus	12	10	.	.	9	1	.	.	.	.	2	25
Lonicera periclymenum	.	5	1	.	1	5	.	.	.	.	1	4
Molinia coerulea	.	1	.	.	.	1	.	.	50	67	4	.
Other graminaceous plants	3	8	.	.	3	1	3	.	.	.	63	68
Pteridium aquilinum	.	.	2	.	.	20	7	12	80	45	55	28
Mosses	.	3	1	7	4	20	1	3	40	100	6	73
Soil texture (%)												
Clay	11	7	4	37	8	7	3	3	3	7	4	4
Silt	38	34	12	30	24	18	8	9	23	24	14	12
Sand	51	59	84	33	68	75	89	88	74	69	82	84
Climate												
Water table (cm)	57	60	55	33	60	51	90	75	31	37	53	82
Moisture deficit (%)	34	44	54	34	69	57	55	38	16	10	78	50
Temperature (°C)	13.3	14.6	14.1	12.9	14.2	15	13.8	13.8	14.4	15.2	15.1	15
Openness of the stand	2	3	2	2	2	3	2	2	4	4	5	4
Humus												
Mean thickness of Ao (cm)	1.1	1.25	1.6	6.5	2.25	3.75	2.5	5.75	11	5.75	1.6	1.4
Mean thickness of AoH (cm)	.	.	0.1	3.75	0.25	1	0.25	2.25	6.5	2	0.6	0.15
pH of A 1	4.8	5	4.5	3.6	4.6	3.7	4	3.5	3.3	3.8	4.1	4.7
Organic matter in A 1 (%)	2.8	3.6	3.5	14.2	4.2	5.6	2.5	6.5	6.2	5.4	4.9	3.6
C/N in A 1	14.8	19	18.5	19.2	22.2	19.2	18.2	29.1	24	26.2	28.5	20.9

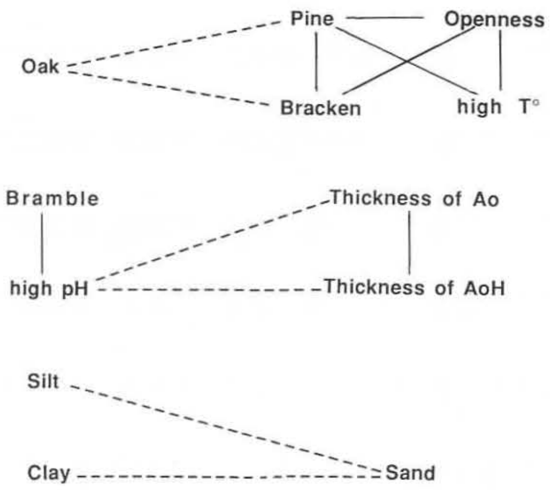

FIG. 1. – Highly associated descriptors (P<0.01) in the twelve studied sites. *Continuous line:* positive association. *Broken line:* negative association.

2) *Interpretation of the axes*

After projecting the site descriptors with the communities and species (*Figs.* 2 and 3), gradients in line with the principal axes are searched for.

The first axis is principally associated with the Clay+/Clay− and Sand+/Sand− oppositions; the highest relative contributions of this axis are for Sand− (RC=0.77), Clay+ (RC=0.72) and Silt+ (RC=0.62). The second axis is principally associated with the pH+/pH− opposition; the highest relative contribution is for pH− (RC=0.50), followed by Honeysuckle− (RC=0.47), Silt− (RC=0.46) and Bramble− (RC=0.45).

Therefore, axes 1 and 2 fit with the soil texture and soil acidity respectively, but it must be emphasized that these two descriptors are not strictly independent. Whereas the first axis mainly opposes clayey and sandy conditions, both of them are opposed to silty conditions on the second axis. Indeed, very clayey or very sandy soils are more acid than silty ones, which produces three distinct poles in the principal plane: clayey and acid, silty and not very acid, sandy and acid.

The third axis is principally associated with the Water+/Water− opposition (RC=0.37 for Water+), while Birch+(RC=0.46), Bracken+ (RC=0.43) and Molinia+ (RC=0.42) have a good representation. But Bracken is an indicator of open stands and, in fact, the Open+/Open− opposition is also fairly parallel to the third axis, notwithstanding a low relative contribution (RC=0.25).

Therefore, axis 3 fits with the depth of the water table and, to a certain extent, the openness of the forest stand. Besides, the display of the descriptors with respect to axes 2 and 3 suggests an association between the presence of a water table and the acidity of the soil, low pH values being more in the direction of hydromorphic sites, and high ones in the direction of well drained sites (*Fig.* 3).

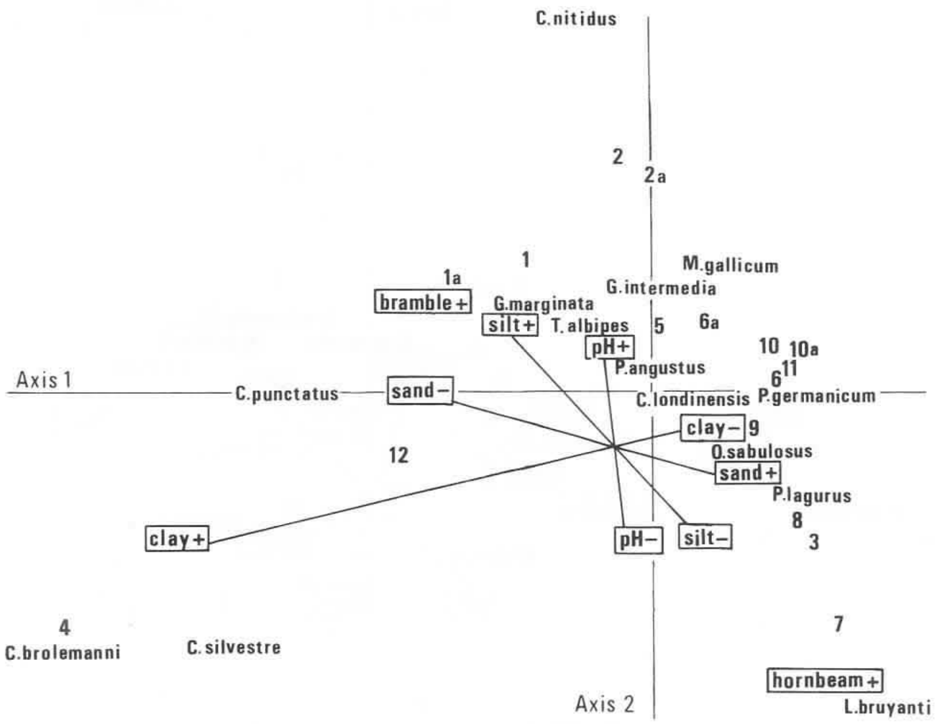

FIG. 2. − Display of Diplopod species, Diplopod communities (numbers) and some site descriptors (framed), with respect to the first and second principal axes of the CA.

A second method makes it possible to justify these interpretations numerically, by calculating coefficients of correlation between the ordinations of the twelve communities (corresponding to the twelve sites) on each axis, and the site descriptors. The most significant linear relations between ordinations and descriptors are shown in figure 4, and confirm the interpretations above:

− the ordination on the first axis is chiefly correlated with clay percentage ($r = -0.85$; $P < 0.01$) and sand percentage ($r = 0.76$; $P < 0.01$);

− the ordination on the second axis is chiefly correlated with silt percentage ($r = 0.62$; $P = 0.05$) and the pH values of the A_1 layer ($r = 0.55$; $P = 0.07$);

− the ordination on the third axis is chiefly correlated with the depth of the water table ($r = 0.73$; $P < 0.01$) and the abundance of Bracken ($r = -0.73$; $P < 0.01$).

As shown in figure 4, all the sites are not near the regression lines. That is the case, for example, for site No. 12, wrongly located in the gradient of soil texture, which means that its Diplopod community is not a valuable indicator of the ecological conditions. In this connection, the low density of community No. 12 (only 12 Ind./m^2) and, thereby, the inaccuracy of its specific composition, must be emphasized. As a result, its peculiar position in the ordinations is not surprising. However, the correlation values indicate that, on the whole, the Diplopod communities are fairly good indicators of the site features.

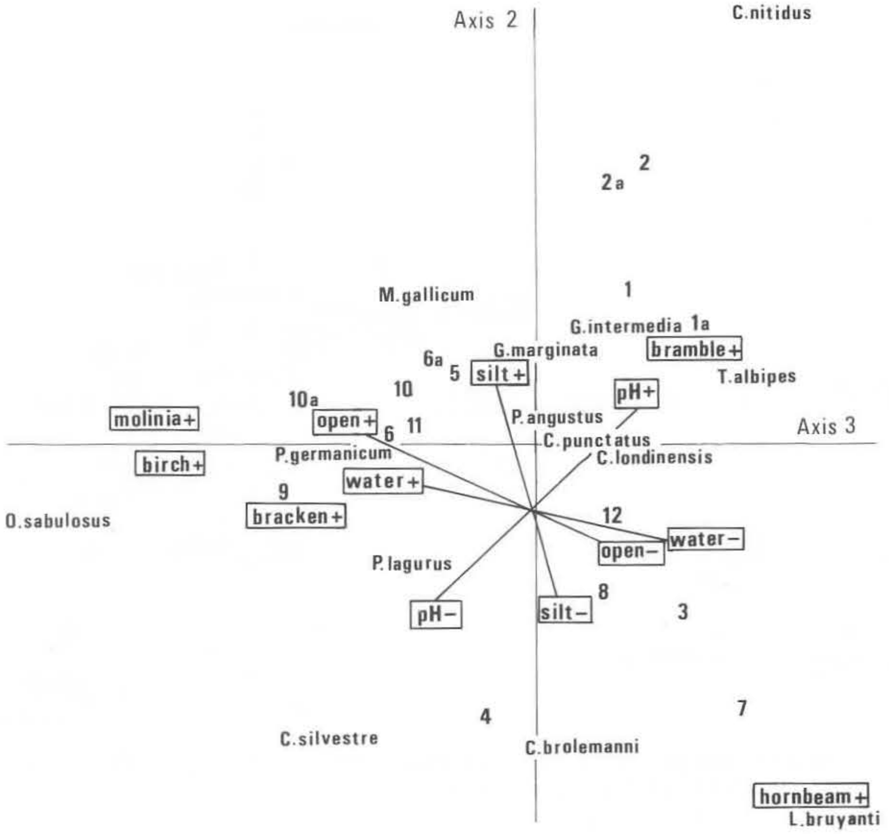

FIG. 3. – Display of Diplopod species, Diplopod communities (numbers) and some site descriptors (framed), with respect to the second and third principal axes of the CA.

3) *Ordinations of the communities and species of Diplopoda*

The three principal axes (soil texture; soil acidity; waterlogging and openness) divide the space into 2^3 subspaces corresponding to various ecological conditions, where the communities and species are displayed (*Figs.* 2 and 3). The supplementary communities (Nos. 1 *a*, 2 *a*, 6 *a* and 10 *a*) are also projected along a certain direction, which is easy to verify by examining the relative contributions of the different axes to them.

The first axis isolates the communities of very clayey sites (Nos. 4 and, in theory, 12) from a set of communities of sandy sites (Nos. 7, 3, 8, 11, 6, 10 and 9); the most characteristic species, known by their high absolute contribution, are *C. brolemanni*, *C. silvestre* and *C. punctatus* at the clayey pole, *L. bruyanti* and *P. germanicum* at the sandy one.

The second axis opposes the communities of sites with an acid humus (Nos. 4 and 7) to the ones of silty sites, with a not very acid humus, the *mull* (Nos. 2, 2 *a*,

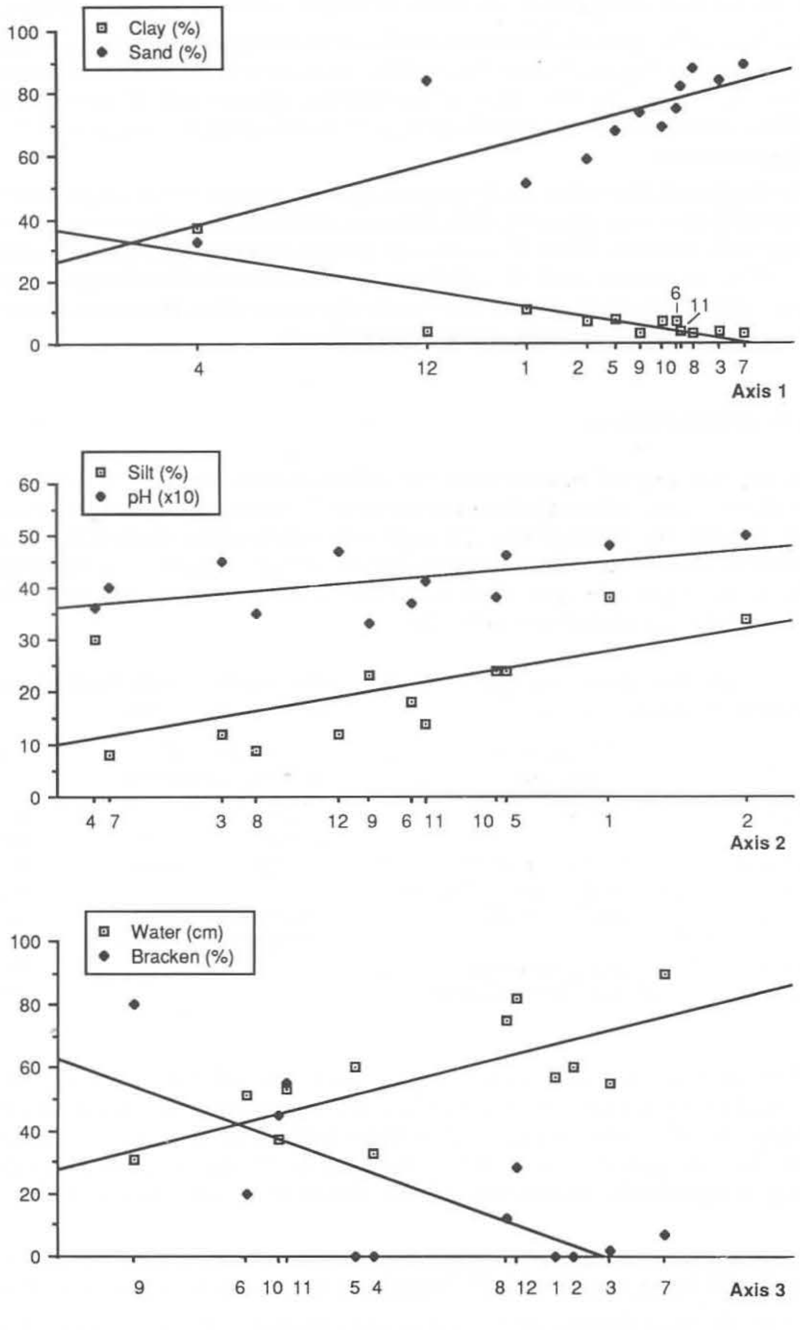

FIG. 4. – Most significant linear relations between the site descriptors and the ordinations of communities on the three principal axes of the CA.

1 and 1 *a*); *C. nitidus* is the characteristic species of sites with high pH values, whereas they are *L. bruyanti*, *C. brolemanni* and *C. silvestre* at the acid pole.

The third axis opposes the communities of waterlogged and open sites (Nos. 9, 10 *a* and, in some degree, 6 and 10), to the ones of well drained and more closed sites (Nos. 7, 3 and 2); the most characteristic species are *P. germanicum* and *O. sabulosus* at the waterlogged and open pole, *L. bruyanti*, *C. nitidus* and *T. albipes* at the opposite one.

The display of the other six Diplopod species, nearer to the origin on the first three axes and therefore not very characteristic, nevertheless gives some information regarding their habitat. Thus *P. lagurus* is always projected along the same directions as *P. germanicum* and *O. sabulosus*, and *G. intermedia* along the same as *C. nitidus*, which reveals tendencies to live in the same sites. However, these species contribute very little to the first three principal axes.

C) Single species analysis

The second way of dealing with the relationships between Diplopod species and site descriptors, is to calculate correlations between these descriptors and the absolute density of populations. Though less informative than CA, it aims at completing it as for non-characteristic species, being present in a wide range of sites. In these cases, the use of correlations is improved by the very fact that species' densities are seldom equal to zero.

TAB. III. — **Site descriptors correlated with the absolute density of the least characteristic Diplopod species** (ns: not significant; *: significant; **: highly significant).

Species	Higher linear correlation	Significant partial correlation	R^2
P. lagurus. . .	pH (−0.71)*	Organic matter % (−0.71)*	0.75**
		or Clay % (−0.70)*	0.75**
G. marginata.	Silt % (+0.73)**	Bramble % (+0.61)*	0.71**
C. londinensis.	Thickness of Ao (−0.81)**	—	0.66**
P. angustus. . .	Silt % (+0.62)*	Sand % (+0.62)*	0.62*
		or Clay % (−0.62)*	0.62*
G. intermedia.	pH (+0.53) ns	—	0.28 ns
M. gallicum. .	Molinia % (+0.49) ns	—	0.24 ns

Table III indicates the descriptors which are correlated with each Diplopod species, as also the proportion of the variation in abundance which can be explained by a linear combination of these descriptors (simple or multiple R^2, as the case may be). In four species out of six, it is possible to find at least one descriptor explaining a significant proportion of the variation in abundance in the studied area:

— the absolute density of *P. lagurus* presents a negative relationship with pH values and, pH being equal, with the organic matter or clay percentage of the soil;

— the absolute density of *G. marginata* presents a positive relationship with the silt percentage of the soil, and this percentage being equal, with the abundance of Bramble;

– the absolute density of *C. londinensis* presents a negative relationship with the thickness of the litter (Ao);

– finally, the absolute density of *P. angustus* presents a positive relationship with the silt and sand percentages of the soil.

In *G. intermedia* and *M. gallicum*, no significant linear relation between the absolute density and the measured site descriptors has been found.

III. . – DISCUSSION

The main habitat dimensions of the Diplopod species in the Ingrannes Massif – *i.e.* their response with respect to the site descriptors being the most critical for their distribution in this area – have been defined. The results are especially interesting when they deal with dominant species, whose high abundances indicate that they find, in some particular sites, favourable conditions to develop and to realize their niche.

A) Habitat of the dominant species

The dominance of several species, *L. bruyanti*, *C. nitidus*, *P. germanicum* and *C. brolemanni*, has been connected with special ecological conditions by means of CA:

– *L. bruyanti* is only abundant in sites with a very sandy soil and an acid humus; these sites are also well drained and closed, generally by a coppice of Hornbeam. It is the first time that some results dealing with this Iulid are published, and many questions arise about them. Notably, what kind of biological benefit may derive from living in acid sites? Are pH values between 3.5 and 4.5 really advantageous to *L. bruyanti*, or is it restricted to such sites because competition is less unfavourable there than in other places? No answer is possible without experimental data, necessary for interpreting the results.

– On the contrary, *C. nitidus* is only abundant in sites with a not very acid humus and a silty soil, namely in humus of *mull* type. Until now, water above all has appeared determining for its distribution, according to literature. Haacker (1968) regards it a a hygrophilous species in the Rhine area, then Biernaux (1972) and Kime & Wauthy (1984) only find it in clayey, fairly humid soils, in the forests of Belgium. Thiele (1959) primarily finds it in calcareous soils ($6.7 \leqq pH \leqq 8$) in the forests of Germany, but admits – as he cannot prove an effect of acidity on its behaviour – that such an association with limestone is indirect, and that it is water conditions of those forest soils which are advantageous to *C. nitidus*: he concludes that it needs high relative humidity, while being sensitive to waterlogging. Pedroli-Christen (1981) comes to the same conclusion in Switzerland. Effectively, the species is characteristic of not very waterlogged sites in the forest of Orleans, but here, the acidity of the soil seems to be the most important dimension of its habitat. This result should be taken into account in further attempts to interpret the distribution of both the Cylindroiulidae, *L. bruyanti* and *C. nitidus*.

– *P. germanicum*, in spite of its high occurrence in the Ingrannes Massif, is only abundant in waterlogged and open sites, with a sandy soil. This species has often been reported in very humid places, and even in water (SCHUBART, 1934; STRIGANOVA, 1975; WEGENSTEINER, 1982). After laboratory experiments, WEGENSTEINER claims that it is due to its low resistance to desiccation, but *P. germanicum* was proved fairly resistant to the drought which occurred in France in 1985 (DAVID, 1990). Consequently, it would be interesting to see whether trophic grounds could not underlie the relationship between this fluid-feeding species and water. In any case, water balance is certainly not the only factor to take into account: evidence of this is given by the absence of *P. germanicum* from site No. 4, which is yet very humid, but also shows a high clay percentage, a dim stand and therefore a weak herb layer. It is possible that one of these three descriptors goes against the Polyzoniid.

– *C. brolemanni* is just the dominant species in this particular, very clayey and closed site, with a very acid humus, where its density amounted to 206 Ind./m^2 in the spring of 1985. It is a unique item of information about the habitat of this Craspedosomatid, and it would be necessary to confirm it before it may be interpreted.

Another species recorded as dominant in two sites, *G. marginata*, is not characteristic of special ecological conditions and proves once again its ubiquity in the forest of Orleans. However, its absolute density is maximum in sites with a silty soil – therefore, indirectly, not very acid. Several authors have found it in contrasting biotops, dry or humid, acid or calcareous (BLOWER, 1956; BROCKSIEPER, 1976; DUNGER & STEINMETZGER, 1981; PEDROLI-CHRISTEN, 1981). After THIELE'S (1959) and HAACKER's (1968) experiments, it has been concluded that the species is unaffected by soil properties (pH, humidity), notably because of its ability to coil, which makes it resistant to dryness. But KIME & WAUTHY (1984) also emphasize the importance of the soil texture for its distribution – a descriptor not noticed beforehand – and conclude that there is a relationship between the abundance of *G. marginata* and the high clay percentages in the forest soils of Belgium. This has to be compared to an aspect of the behaviour of Glomeridae mentioned in literature (VERHOEFF, 1910; SCHUBART, 1934) and frequently observed in site No. 1: females lay their eggs upon the soil and protect them with a mineral mixture, being more made up of fine clay or silt particles than of grains of sand.

B) Habitat ot the least abundant species

The other Diplopod species are also more or less associated with some descriptors, but the results lose a part of their interest in so far as the populations are less abundant, and one cannot be certain to have found them in optimal conditions. Nevertheless, soil acidity seems to play an important role in the habitat of several species. Some mainly live in sites with a very acid humus, such as:

– *P. lagurus*, mostly present under bark, but also in litter over acid and not too clayey soil;

– *C. silvestre*, in acid and clayey soil; this distribution is at variance with some statements about its preference for neutral or basic soil (DUNGER & STEINMETZGER, 1981); however, it has been reported as very abundant in an acid peat bog by PEDROLI-CHRISTEN (1977).

On the contrary, some species mainly live in sites with a silty soil and a not very acid humus, such as:

– *C. londinensis*, that BLOWER (1956) even regards as a species characteristic of base-rich soils;

– *P. angustus*, which was even dominant in the *mull* site No 1 before the drought of 1985 (community No. 1 *a*);

– *G. intermedia*, whose habitat dimensions, although not quite clear in the Ingrannes Massif, resemble those of *C. nitidus*; THIELE (1959) and KIME & WAUTHY (1984) underscored the same phenomenon, the first author interpreting the co-occurrence of both these species with the help of climate, and the latter with the help of soil texture.

The habitat of other not very abundant species seems to be related to either the absence of a water table – in *T. albipes*, in accordance with HAACKER (1968) and PEDROLI-CHRISTEN (1981) –, or the presence of a water table – in *O. sabulosus* and perhaps *M. gallicum* –, or else the soil clay percentage – curiously enough in *C. punctatus* which lives most of the time in rotting wood.

C. Biogeographical limits

The principal axes of variability found with the help of CA (soil texture, soil acidity, waterlogging and openness) strictly depend on the initial data, and could hardly be extrapolated. In the Ingrannes Massif, the data from the twelve sites are believed exhaustive enough to ensure that the results would not be questioned by further studies in the same area – at least with regard to the main Diplopod species. But the habitat dimensions of the species defined in these special conditions, cannot be extended to very different areas. As an example, suppose – pure hypothesis – that a species is incapable of developing in soils whose pH value is below 4.5, and thereby is characteristic of not very acid sites in the forest of Orleans; it is conceivable that, in another area on calcareous soil, the acidity of humus will no longer appear critical for its distribution; the species could even be characteristic of the most acid sites if the highest pH values were also unfavourable to its development. This example emphasizes the futility of classing species according to their acidophilia, thermophilia, xerophilia, etc., until their whole range has been surveyed and analysed – not only as to their presence, but also as to their abundance. Even then, those terms could be proved unusable, because populations undergoing different selective pressures can evolve towards various adaptations; and so, two populations of the same species living in different ecological backgrounds, might respond to a given stimulus in various ways. A frequent use of qualifiers such as "acidophilous", "thermophilous", etc., in articles dealing with Diplopoda, brings out the importance of typological thought in Ecology. Actually, the habitat dimensions defined in this study are only valid within the limits of a temperate forest, with acid and more or less waterlogged soils, which must be kept in mind when comparing the results to those of other authors.

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SUMMARY

Twelve sites in the forest of Orleans (France) are described, and the relationships between the site descriptors and the composition of the Diplopod communities are studied. These relationships are underscored with the help of an *ad hoc* application of correspondence analysis. The interpretation of three principal axes as ecological gradients, statistically checked, indicates that they fit with soil texture, soil acidity, and waterlogging respectively, the most characteristic Diplopod species being segregated along these axes. The distribution of the least characteristic Diplopod species is also related to the site descriptors with the help of total and partial correlations. Soil acidity appears to be an important habitat dimension for many species. However, some results are not fully consistent with literature, which underlines the necessity of breaking with a typological point of view in this kind of study.

RÉSUMÉ

Dimensions de l'habitat des Diplopodes dans une forêt tempérée sur sols acides

Douze stations de la forêt d'Orléans (France) sont décrites afin d'étudier les relations entre les descripteurs stationnels et la composition des peuplements de Diplopodes. Ces relations sont d'abord mises en évidence par analyse factorielle des correspondances. L'interprétation des trois premiers axes principaux en termes de gradients écologiques (interprétation contrôlée statistiquement) montre qu'ils correspondent respectivement à la texture, à l'acidité et au degré d'hydromorphie du sol. L'ordination des espèces de Diplopodes le long de ces axes permet d'identifier les espèces les plus caractéristiques. Pour les espèces les moins caractéristiques, l'étude est complétée par le calcul des corrélations totales et partielles avec les descripteurs stationnels, ce qui confirme l'importance de l'acidité du sol pour l'abondance de plusieurs espèces. La discussion met notamment en garde contre une extrapolation hâtive de ces résultats à d'autres régions dans une optique typologiste.

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